

Effects of girdling on stem CO₂ efflux and its temperature sensitivity in Chinese fir and sweetgum trees

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ABSTRACT

The effect of carbohydrate supply on stem CO₂ efflux and its temperature sensitivity is crucial in predicting forest carbon cycling under climate change and forest management but has been rarely reported. In this study, we altered carbohydrate supply via stem girdling and investigated the effect of nonstructural carbohydrate concentration on stem CO₂ efflux and its temperature sensitivity in Chinese fir and sweetgum trees in spring and winter. The stem CO₂ efflux of Chinese fir increased significantly above the girdle in spring and winter, but decreased below the girdle in winter. The stem CO₂ efflux of sweetgum increased above the girdle and decreased below the girdle in spring but not in winter. Seasonal variations in the response of stem CO₂ efflux to girdling were associated with the changes in stem soluble sugar and starch concentration, especially in sweetgum tree. Girdling altered Q_{10} of the stem CO₂ efflux, and this effect was dependent on location, season and species. Compared with the Q_{10} of the stem CO₂ efflux in non-girdled trees, that of CO₂ efflux in Chinese fir increased by 45% above the girdle but decreased by 16% below the girdle in winter. These values also exhibited 6% and 11% responses in spring. By contrast, the Q_{10} of the stem CO₂ efflux in sweetgum increased by 95% above the girdle and decreased by 45% below the girdle in spring. However, these values were nearly constant in winter. We concluded that the effect of carbohydrate supply on stem CO₂ efflux and its temperature sensitivity depends on season and species. Therefore, the vital role of carbohydrate supply that regulates stem CO₂ efflux and its temperature sensitivity should be considered for the understanding and modeling of forest carbon cycling response to forest management, especially under global climate changes.

1. Introduction

Stem CO₂ efflux, the diffusion of CO₂ from woody stems to the atmosphere, plays a pivotal role in the carbon cycle of forest ecosystems (Ryan et al., 1996; Bowman et al., 2008; Teskey et al., 2008). Yang et al. (2016a) estimated that 6.7 Pg C year⁻¹ is released to the atmosphere via stem CO₂ efflux, accounting for 20% of the net primary production from global forest ecosystem. The contribution of stem CO₂ efflux to ecosystem respiration is 8% in boreal forests and up to 27% in tropical forests (Yang et al., 2016a). Different from other ecosystem respiration components, such as soil CO₂ efflux (Luo and Zhou, 2006; Bond-Lamberty and Thomson, 2010), stem CO₂ efflux is still poorly understood. Stem CO₂ efflux is a combination of the CO₂ released directly to

the atmosphere by respiring cells (including phloem, cambium, and ray cells) in stems (Teskey et al., 2008; Trumbore et al., 2013) and the transported CO₂ diffused from the xylem sap (McGuire and Teskey, 2004; Teskey and McGuire, 2007; Aubrey and Teskey, 2009; Bloemen et al., 2013; Salomón et al., 2016). The relationship between stem CO₂ efflux and carbohydrate supply (Wertin and Teskey, 2008; Maier et al., 2010) has received less attention than that between stem CO₂ efflux and temperature or water stress (Yang et al., 2012a,b; Rodríguez-Calcerrada et al., 2014; Rowland et al., 2018; Zhao et al., 2018). Thus, the effect of carbohydrate supply on stem CO₂ efflux should be studied because carbohydrate supply is altered by global climate change, such as increasing CO₂ concentration or drought, and forest management processes, such as thinning or pruning.

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Stem CO₂ efflux is linearly related to gross primary production at the ecosystem (Zha et al., 2004) and global scales (Yang et al., 2016a), suggesting that photosynthetic rates, carbohydrate availability, and stem CO₂ efflux are tightly coupled. Previous studies reported that an increase in CO₂ concentration increases net photosynthesis, and further stem CO₂ efflux in saplings (Wertin and Teskey, 2008) and adult trees (Edwards et al., 2002). Forest management processes, such as pruning or fire, also affect stem CO₂ efflux by altering the carbohydrate supply (Ogawa, 2006; Clinton et al., 2011). The notion that carbohydrate supply controls stem CO₂ efflux has also been demonstrated via physiological girdling (Johnsen et al., 2007) and physical girdling (Ogawa, 2006; Maier et al., 2010; Maunoury–Danger et al., 2010). Maier et al. (2010) observed a positive relationship between temperature-corrected stem CO₂ efflux and carbohydrate concentration. However, Yang et al. (2015) found that pruning significantly reduces stem CO₂ efflux, but does not affect carbohydrate concentration.

The temperature sensitivity (Q_{10}) of stem CO₂ efflux is defined as a factor at which the rate increases with a 10 °C rise in temperature. The Q_{10} of stem CO₂ efflux is assumed to be equal ($Q_{10} = 2$) and independent of carbohydrate availability in most ecosystem models (Thornley and Cannell, 2000). Atkin and Tjoelker (2003) proposed that carbohydrate availability may affect the Q_{10} of respiration. Stem respiration is catalyzed by plant respiratory enzymes in accordance with simple Michaelis–Menten kinetics (Davidson et al., 2006). The maximum rate of enzyme activity (V_{max}) and the half-saturation constant (K_m) depend on temperature. Thus their respective temperature sensitivities are cancelled when stem physiological metabolism is C-limited. Therefore, the Q_{10} of respiration may increase when substrate availability increases. This phenomenon is supported by the finding that the Q_{10} of stem CO₂ efflux respectively increases and decreases above and below the girdle because of the altered carbohydrate availability in *Pinus taeda* (Maier et al., 2010). By contrast, Ogawa (2006) reported that girdling does not affect the Q_{10} of stem CO₂ efflux in *Pinus sylvestris*. Thus, the influence of carbohydrate availability on the temperature sensitivity of stem CO₂ efflux should be studied to model forest ecosystem carbon budgets and predict the effects of climate change and forest management on these processes.

In this study, we conducted an experiment to examine the effect of girdling on stem CO₂ efflux and its temperature sensitivity in Chinese fir (*Cunninghamia lanceolata*) and sweetgum (*Liquidambar formosana*) trees in spring (rapid diameter growth) and winter (diameter growth ceased). This study specifically aimed to test the following hypotheses: (1) girdling affects stem CO₂ efflux by altering carbohydrate availability; (2) the response of stem CO₂ efflux to girdling is dependent on season; and (3) the temperature sensitivity of stem CO₂ efflux is associated with girdling-induced changes in carbohydrate availability.

2. Materials and methods

2.1. Site description

This study was conducted at the Huitong Experimental Station of Forest Ecology, Hunan Province, China (26°40′–27°09′ N and 109°26′–110°08′ E). This site is characterized by a typical humid climate of mid-subtropical monsoon. The average annual precipitation in this area is approximately 1200 mm. The average annual temperature is 16.5 °C, and the average temperatures in January and July are 1.9 °C and 29.0 °C, respectively. The parent material in this site is shale, which is classified as an oxisol according to the second edition of the U.S. Soil Taxonomy. Girdling experiments were conducted in a Chinese fir plantation and a secondary forest. The Chinese fir plantation was established in early spring in 1990 with a planting density of 2000 stems ha⁻¹. The secondary forest was mostly regenerated in around 1980 and was dominated by native broadleaved tree species, including *Castanopsis hystrix*, *L. formosana*, *Cyclobalanopsis glauca*, *Machilus pauhoi*, and *Juglans cathayensis*, which are approximately 50 m away

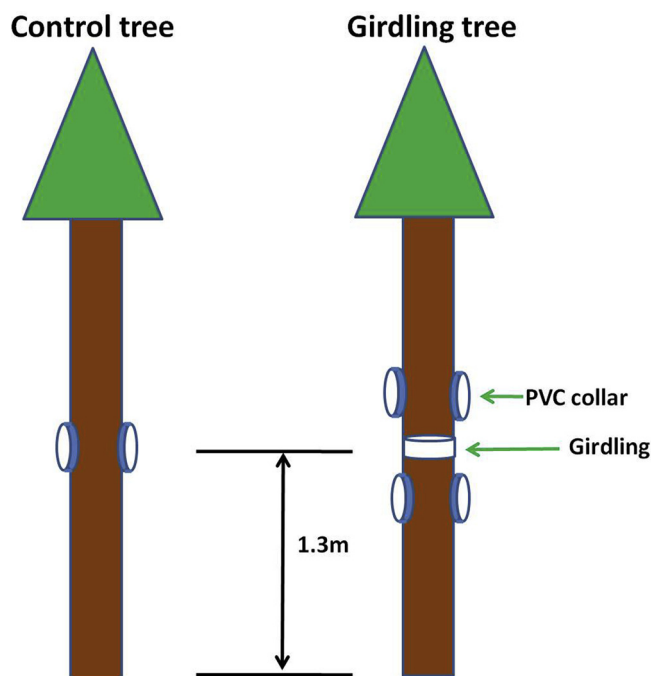


Fig. 1. Schematic showing the placement of stem CO₂ efflux chambers and girdling treatment.

from the Chinese fir plantation.

2.2. Stem CO₂ efflux measurement

Six trees from the Chinese fir plantation were selected to measure stem CO₂ efflux during spring and winter 2014, respectively. The selected sample trees were relatively uniform based on diameter at breast height and tree height. Three randomly selected trees in each season were girdled, and the remaining three served as a control. Stem CO₂ efflux was examined using a horizontally oriented soil chamber technique in accordance with previously described methods (Xu et al., 2000). A stem and a soil CO₂ efflux chamber (Li-Cor Li-6400-09 units) were connected by attaching a custom-built polyvinyl chloride (PVC) collar (inside diameter of 10 cm) to the stem surface. One end of the PVC collar was cut flat to connect to the Li-Cor Li-6400-09 units and the other end was cut to suit to the approximate stem curvature. The loose bark from the area, where the curved end of the PVC collar would be attached to the stem, was removed carefully. Two PVC collars were fastened on the right and left sides of the stem at a height of ca.1.3 m by using a silicone sealant for each control tree. Four collars were fastened on the stem at a height of ca.1.1 and ca. 1.5 m for the girdled tree (Fig. 1). Stem CO₂ efflux was measured from 09 : 00 h and 11 : 00 h by using the Li-Cor Li-6400-09 units. The measurements were taken 2 days before girdling to establish pregirdling conditions. The trees were girdled by carefully removing 5 cm of the bark and the phloem all around the stem at a height of ca.1.3 m by using a rasp (Fig. 1). Stem CO₂ efflux was measured from day of year (DOY) 142 to DOY173 in 2014 in spring and from DOY 347 in 2014 to DOY 26 in 2015 in winter. The temperature of the stems at a depth of 3 cm was simultaneously measured using a temperature sensor probe attached to the Li-Cor Li-6400-09 units. Six sweetgum trees from the secondary forest were also selected for spring and winter girdling experiments, respectively. Stem CO₂ efflux and stem temperature were continuously measured for 1 month after girdling during spring (DOY 112–143 in 2014) and one and a half months during winter (DOY 347 in 2014 to DOY 26 in 2015). The stem CO₂ efflux of the sweetgum tree was not measured from DOY 117 to DOY 130 in 2014 because of equipment malfunction.

2.3. Nonstructural carbohydrate (NSC)

Six surrounding control and girdled trees that were similar to the trees from which the stem CO₂ efflux was measured, were selected to measure stem NSC (soluble sugar plus starch) for each species and season to avoid affecting the measurement of stem CO₂ efflux. The stem bark at breast height in the control trees and the stem bark above and below the girdle in the girdled trees were sampled between 09 : 00 h and 11 : 00 h to minimize diurnal variation in carbohydrate concentration (Edwards and McLaughlin, 1978). The samples were immediately placed in a cooler and transported to our laboratory. Soluble sugar and starch were analyzed through an enzymatic assay (Bergmeyer et al., 1988; McCleary et al., 1997). A detailed description can be found in our other studies (Yang et al., 2016b).

2.4. Data analysis

The girdling effect (GE) of the stem CO₂ efflux on different positions (above the girdle: Ga; below the girdle: Gb) was calculated using the following equation:

$$GE = 100 \times \frac{E_{\text{treatment}} - E_{\text{control}}}{E_{\text{control}}} \quad (1)$$

where E_{control} and $E_{\text{treatment}}$ denote the stem CO₂ efflux under the control and girdling treatments, respectively.

The relationship between stem CO₂ efflux (E) and stem temperature (T) was modeled by the following exponential equation:

$$E = ae^{bT} \quad (2)$$

Q_{10} was used as a parameter of the temperature sensitivity of stem CO₂ efflux through the following equation:

$$Q_{10} = e^{10b} \quad (3)$$

The average stem CO₂ efflux from the two chambers (the right and left sides of the stem) was used for analysis. Repeated measures ANOVA was performed to determine the effects of girdling treatment and sampling date on stem CO₂ efflux, stem temperature, soluble sugar and starch concentration. The relationship between the girdling effect values of stem CO₂ efflux and the days after girdling was fitted with a linear or quadratic equation. Individual Q_{10} was then calculated for each tree by using Eqs. (2) and (3). Two-way ANOVA was performed to determine the effects of girdling treatment and season on Q_{10} . Statistical analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Chinese fir girdling experiment

Stem temperatures ranged from 17.9 °C to 27.9 °C in the girdling experiment performed during spring and from 2.7 °C to 14.4 °C during winter. Girdling did not affect stem temperature in both seasons (Fig. 2a, e) but significantly affected the stem CO₂ effluxes in both seasons (Fig. 2b, f; spring: $P = 0.03$; winter: $P = 0.001$). Girdling treatment and date elicited a significant interactive effect on stem CO₂ effluxes, indicating that the increase in this parameter with girdling time was significantly different among the girdling treatments, being more remarkable increase in Ga, and less decrease in Gb during spring and winter (Fig. 2b, f). Soluble sugar and starch concentrations did not significantly differ among the treatments during spring (Fig. 2c, d). By contrast, the starch concentration significantly increased in Ga during winter, but the soluble concentration did not (Fig. 2g, h).

3.2. Sweetgum girdling experiment

Stem temperatures ranged from 15.1 °C to 22.7 °C and were

unaffected by spring girdling treatment (Fig. 3a; $P = 0.96$). Stem CO₂ efflux significantly increased above the girdle and decreased below the girdle after the girdling treatment during spring (Fig. 3b). Thirty days after girdling (DOY 142), the stem CO₂ efflux in Ga increased by 127%, whereas that in Gb decreased by 36%, compared with that in the control. Girdling caused soluble sugar accumulation in Ga ($26.58 \pm 2.76 \text{ mg g}^{-1}$), and soluble sugar depletion in Gb ($17.10 \pm 0.89 \text{ mg g}^{-1}$), compared with those in the control ($21.75 \pm 1.28 \text{ mg g}^{-1}$; Fig. 3c). The starch concentration also increased in Ga but decreased in Gb after girdling (Fig. 3d). The starch concentration in Ga was significantly higher ($P = 0.006$) than that in the control (10.64 mg g^{-1}), but not in Gb ($P = 0.342$). However, after winter girdling no significant difference was observed in stem temperatures (Fig. 3e; $P = 0.88$), stem CO₂ efflux (Fig. 3f; $P = 0.94$), soluble sugar concentration (Fig. 3g; $P = 0.85$), and starch concentration (Fig. 3h; $P = 0.21$) among the treatments.

3.3. Girdling effect

The girdling effect values of Ga in Chinese fir trees were hump-shaped with the maximum values obtained on the 17th day after girdling during spring and on the 29th day after girdling during winter (Fig. 4a). By contrast, the significantly negative linear correlation between the girdling effect values and the day after girdling for Chinese fir tree was detected in Gb both during spring and winter. The girdling effect values for sweetgum tree were correlated positively with the day after girdling in Ga, whereas these values were negatively correlated in Gb in the girdling experiment during spring (Fig. 4b). By contrast, the girdling effect values were not significantly correlated with the day after girdling in Ga and Gb during winter.

3.4. Temperature sensitivity

The Q_{10} of stem CO₂ efflux in Chinese fir trees was significantly affected by girdling in winter, but was nearly constant in spring (Fig. 5a). Compared with that in the control (2.59 ± 0.27), Q_{10} increased significantly above the girdle (3.74 ± 0.19) but not below the girdle (2.17 ± 0.03) during winter. By contrast, the Q_{10} of stem CO₂ efflux in sweetgum tree was significantly affected by girdling treatment during spring, but not during winter (Fig. 5b). The Q_{10} (4.65 ± 0.36) of stem CO₂ efflux in Ga was almost two times higher than that in the control (2.38 ± 0.46) during spring. The Q_{10} (1.31 ± 0.46) decreased remarkably but not significantly in Gb compared with that in the control during spring.

4. Discussion

4.1. Response of stem CO₂ efflux to girdling

In support of our first hypothesis, our results revealed that girdling significantly affected stem CO₂ efflux (Figs. 2–4). Consistent with our findings, previous studies indicated that stem CO₂ efflux strongly responds to physiological (via phloem chilling) or physical girdling (Johnsen et al., 2007; Maier et al., 2010). This phenomenon was possibly caused by the accumulation of soluble sugars and starch above the girdle and by the depletion of these substances below the girdle after girdling because the availability of recently formed photosynthates is an important factor controlling stem CO₂ efflux rates. Another possible explanation for the changed stem CO₂ efflux is sap flow modified by girdling, because the CO₂ derived from the stem or root respiration is dissolved and transported internally through the xylem (Teskey et al., 2008; Bloemen et al., 2013). However, previous studies confirmed that short-term girdling may terminate only the photosynthate supply through the phloem, and can still enable water transport through the xylem (Högberg et al., 2001; Subke et al., 2011). For example, Maier and Clinton (2006) did not find any change in the sap flow of pine (P.

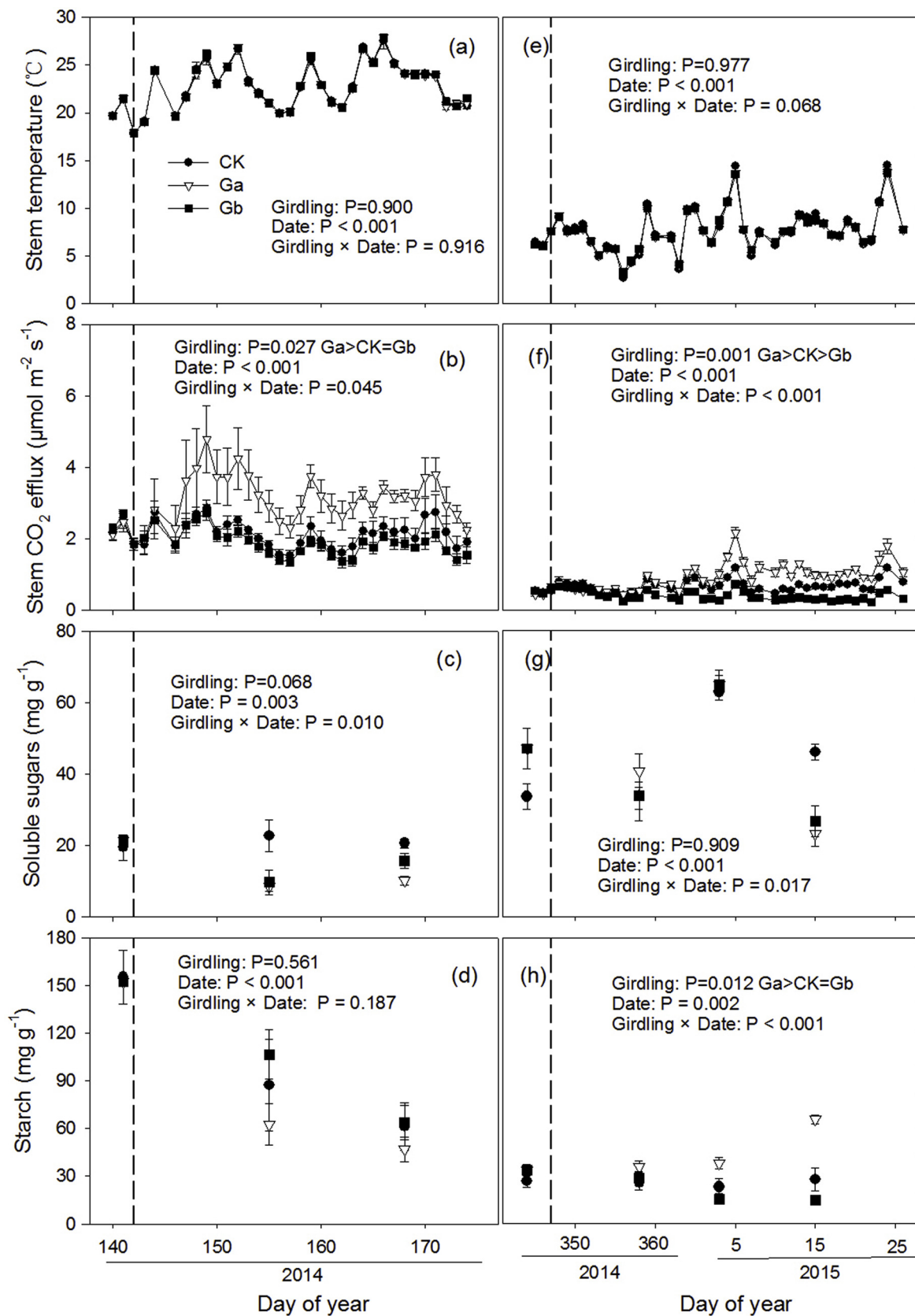


Fig. 2. Effect of girdling on stem temperature (a, e), stem CO_2 efflux (b, f), soluble sugar concentration (c, g), and starch concentrations (d, h) during spring (a, b, c and d) and winter (e, f, g and h) in Chinese fir trees. Bars represent the standard errors of the mean for each treatment ($n = 3$). Dashed line represents the date when girdling was performed. CK, control (closed circles); Ga, above girdle (open triangles); and Gb, below the girdle (closed squares).

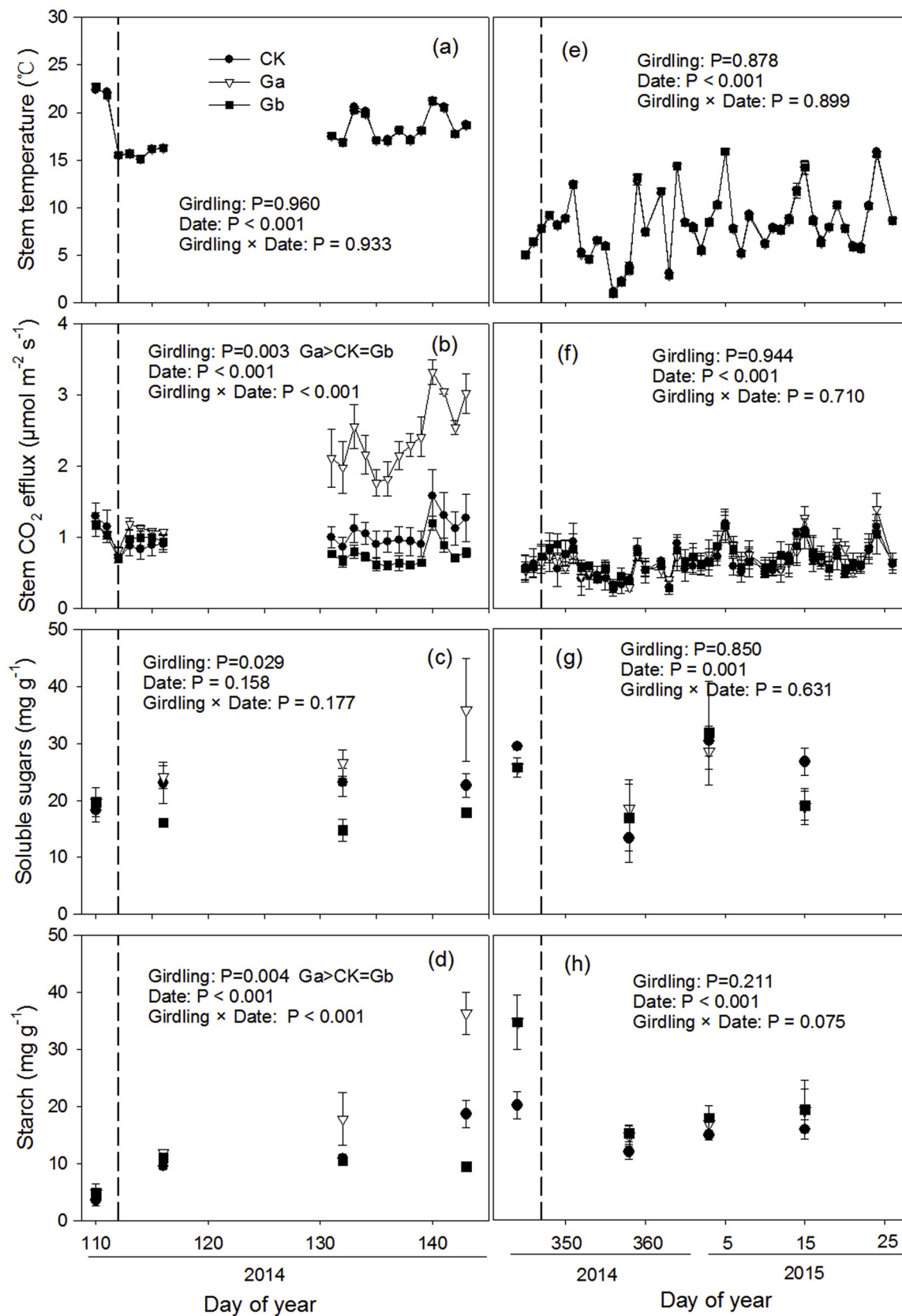


Fig. 3. Effect of girdling on stem temperature (a, e), stem CO₂ efflux (b, f), soluble sugar concentration (c, g), and starch concentrations (d, h) in spring (a, b, c and d) and winter (e, f, g and h) in sweetgum trees. Bars represent the standard errors of the mean for each treatment ($n = 3$). Dashed line represents the date when girdling was performed. CK, control (closed circles); Ga, above girdle (open triangles); and Gb, below the girdle (closed squares).

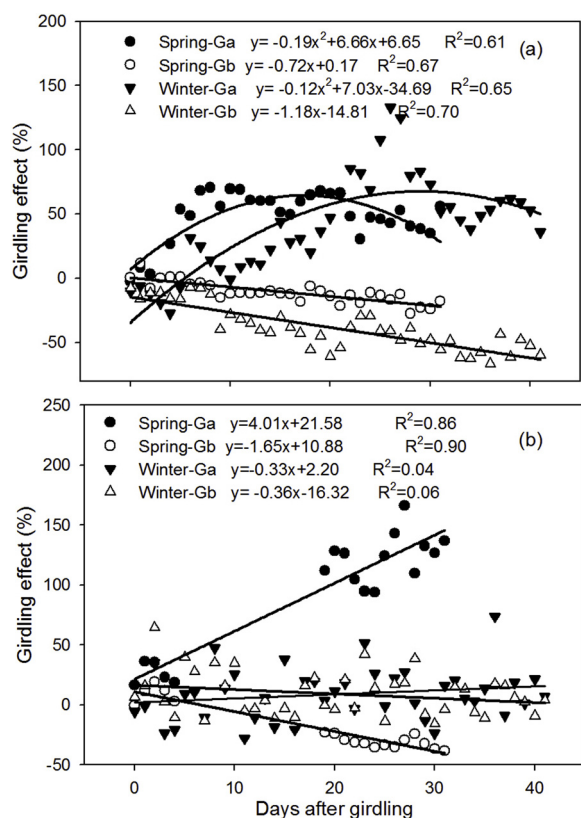


Fig. 4. Variation in the girdling effect of stem CO₂ efflux in Chinese fir tree (a) and sweetgum tree (b). Ga, above girdle in spring (closed circles) and in winter (closed triangles); and Gb, below the girdle in spring (open circles) and in winter (open triangles).

taeda) in a stem-girdling experiment. In the present study, although the sap flow of Chinese fir was not measured, stem CO₂ efflux showed different responses above and below the girdle, indicating indirectly that the change in stem CO₂ efflux after girdling was not attributed to the effects of girdling on sap flow.

We observed the different effects of girdling on stem CO₂ efflux in degree and timing with season (Figs. 2–4), which was in line with our second hypothesis. The soluble sugars accumulated above the girdle because phloem transport was hindered by girdling. Soluble sugars have three possible outcomes: can be incorporated into growth, transferred to storage, or rapidly respired. In Chinese fir, stem or canopy growth could consume excess sugar above the girdle during spring but not during winter because these parts are strong carbon sinks. In our current study, stem radial growth was not measured. However, previous studies also reported that stem radial growth above the girdle was accelerated during growing season (Maier et al., 2010; Maunoury-Danger et al., 2010). The transfer of excess sugars into storage was impossible in Chinese fir during spring, because our result showed that starch content decreased with time (Fig. 2d). By contrast, we found that the starch content above the girdle during winter increased with time (Fig. 2h), suggesting that the transfer of sugars into storage is an important pathway of Chinese fir during non-growing season. In addition, carbohydrate accumulation can reduce photosynthesis, as confirmed by previous studies (Johnsen et al., 2007; Urban and Alphonsout, 2007). Thus, the excess carbohydrate was rapidly respired to decrease the feedback inhibition of photosynthesis, and this observation possibly explained the increase in stem CO₂ efflux above the girdle in both seasons to a certain extent. We found that the stem CO₂ efflux above the girdle increased until a threshold was reached, and then decreased in both seasons. The time to initiate the decrease in stem CO₂ efflux during winter was longer than that during spring (Fig. 4). In

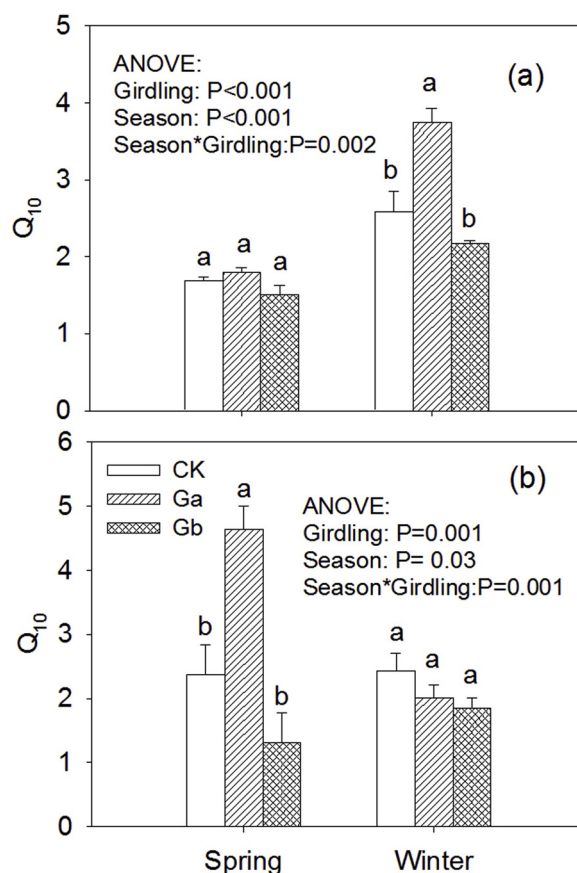


Fig. 5. Effect of girdling on Q_{10} (temperature sensitivity of stem CO₂ efflux) in Chinese fir trees (a) and sweetgum trees (b). Bars represent the standard errors of the mean for each treatment ($n = 3$). CK, control (closed circles); Ga, above girdle (open triangles); and Gb, below the girdle (closed squares).

sweetgum trees, stem CO₂ efflux, soluble sugar and starch content above the girdle increased with time during spring, but not during winter (Fig. 3). This finding indicated that all of the three potential paths are involved in consuming excess sugar above the girdle during the growing season.

In Chinese fir, the decline in stem CO₂ efflux below the girdle was more rapid and larger during winter than during spring, because the former had a steeper slope of GE than the latter (Fig. 4a). Maier et al. (2010) also observed a similar seasonal response to girdling in stem CO₂ efflux in loblolly pine. The different effects of girdling on stem CO₂ efflux below the girdle with season were possibly due to the differences in starch availability. In our study, the starch concentrations in Chinese fir were high during spring (Fig. 2d, h). Thus, when photosynthate supply was terminated, the muted reduction in stem CO₂ efflux below the girdle indicated the support of stored carbohydrates to stem respiration in the absence of current photosynthates. In winter, the starch concentrations were low, and the remarkable decline in stem CO₂ efflux below the girdle implied that the maintenance respiration of the stem at this time of the year was dependent primarily on the availability of the current photosynthates. By contrast, the girdling effect of stem CO₂ efflux in sweetgum tree was less prominent during winter than that during spring (Fig. 3). Considering that sweetgum is a deciduous tree species, the negligible effect of girdling in winter is reasonable because no current photosynthate supply was provided at this time of the year.

4.2. Response of Q_{10} to girdling

In this study, the Q_{10} of stem CO₂ efflux in the control treatment was comparable with that observed in other species (Yang et al., 2012a,b;

Rodríguez-Calcerrada et al., 2014; Tu et al., 2017; Darenova et al., 2018). However, we found that girdling altered the Q_{10} of stem CO_2 efflux of both species (Fig. 5), and this observation was consistent with our third hypothesis. To a large extent, these results might be explained by the altered carbohydrate availability after girdling. In general, tissue-level respiration is associated with enzyme availability and metabolic substrate (Pruyn et al., 2005), and stem physiological metabolism is normally C-limited (Edwards et al., 2002; Wertin and Teskey, 2008). Considering the theoretical relationship between the availability of substrate and the temperature sensitivity of respiration based on a Michaelis–Menten model, which is widely used to study enzyme kinetics (Davidson et al., 2006), we suggest that the increased Q_{10} of the stem CO_2 efflux above the girdle is attributed to the effect of girdling on carbohydrate availability. This notion was supported by our results that Q_{10} of the stem CO_2 efflux increased when the starch accumulated above the girdle in Chinese fir (Figs. 2h and 5a), and when the soluble sugars and starch accumulated above the girdle in sweetgum (Figs. 3c, d and 5b).

The effect of girdling on the temperature sensitivity of stem CO_2 efflux above the girdle depended on season (Fig. 5). In our study, Q_{10} , which was derived from field data, reflected the apparent temperature sensitivity by confounding multiple factors and physiological processes (Yang et al., 2012b). Therefore, the different seasonal responses of apparent Q_{10} might be attributed to the seasonal shift in the relative importance of maintenance respiration and growth respiration, because maintenance respiration is temperature sensitive (Brito et al., 2010), whereas growth respiration is temperature independent (Ryan et al., 1994). For Chinese fir, a conifer species, the strong girdling effect on Q_{10} above the girdle in winter suggested that maintenance respiration dominated the stem CO_2 efflux during the non-growing season. By contrast, the lack of girdling effect on Q_{10} in spring indicated that the majority of the increased stem CO_2 efflux above the girdle was related to growth, and growth respiration confused the apparent Q_{10} . Large girdling effect on Q_{10} in non-growth season, but not in growth season, was also found in other conifer species (Maier et al., 2010). In contrast to the girdling effect on Q_{10} in Chinese fir, the girdling effect on Q_{10} in sweetgum, a deciduous species, was more pronounced during spring than during winter (Fig. 5b). The different seasonal patterns of the effect of girdling on Q_{10} might be partly attributed to species differences. As a fast-growing timber species, Chinese fir may incorporate most of the soluble sugars accumulated above the girdle into growth. However, this condition does not occur in sweetgum, because part of the accumulated soluble sugars is transferred to storage, as indicated by the increase in starch content above the girdle (Fig. 3d). Therefore, we presumed that growth respiration elicited a negligible effect on apparent Q_{10} above the girdle in sweetgum.

Girdling had a negligible effect on Q_{10} of stem CO_2 efflux below the girdle in both species (Fig. 5). In contrast to our results, previous findings indicated that the Q_{10} of stem CO_2 efflux decreases below the girdle in loblolly pine (Maier et al., 2010). These contradictory results may be attributed to the following reasons. First, the response of non-structural carbon to girdling was less prominent below the girdle than above the girdle in our current study. For example, forty-five days after girdling starch concentration increased by 136% above the girdle and decreased by 46% below the girdle relative to the non-girdled Chinese fir trees in winter (Fig. 2d and h). Second, the potential effects of sap flow might contribute to these contradictory results, because CO_2 movement in the xylem stream may strongly affect the Q_{10} of stem CO_2 efflux (Zhu et al., 2012). Maier et al. (2010) estimated Q_{10} by using the nighttime data, and eliminated the effects of sap flow. In our study, stem CO_2 efflux was measured once during the day. Therefore, the absence of the reduced in Q_{10} below the girdle might be partly due to the potential effects of sap flow.

4.3. Implications

In China, Chinese fir and sweetgum are the most important timber species that produce timber and mitigate greenhouse gas emissions through carbon sequestration. Global climate changes (such as elevated CO_2 , warming, and drought etc.) and plantation management (such as thinning and pruning practices) can affect stem CO_2 efflux by altering canopy photosynthesis and substrate supply (Edwards et al., 2002; Rodríguez-Calcerrada et al., 2014; Yang et al., 2015), and consequently affecting ecosystem effluxes and carbon sequestration capacity. Therefore, understanding how substrate availability controls stem CO_2 efflux and its temperature response is necessary in constructing and modeling plant and ecosystem carbon budgets and in predicting the effects of climate change and plantation management on ecosystem carbon cycling and its feedback to the climate system through respiration (IPCC, 2013). The notion that carbohydrate supply can alter stem CO_2 efflux and its temperature response has been confirmed in our study and other studies (Edwards et al., 2002; Maier et al., 2010). The current study provided some evidences to highlight the importance of carbohydrates in driving stem CO_2 efflux. However, carbohydrate status is quite complex (involving amount, form, and mutual conversion of soluble sugar and starch), and is closely related to many ecological processes, such as growth rate and phenology, which are not measured in our study. Therefore, how substrate availability, growth phenology and other related physiological processes control the stem CO_2 efflux and its temperature response must be studied in the future.

5. Conclusions

The altered carbohydrate supply via stem girdling significantly affected the stem CO_2 efflux and its temperature sensitivity in Chinese fir and sweetgum tree. The different potential fates of soluble sugars that accumulated above the girdle and the starch availability below the girdle might result in the differences in stem CO_2 efflux with regard to degree and timing with season. The increasing carbohydrate availability above the girdle also increased the apparent Q_{10} . However, this response was dependent on season possibly because of the seasonal shift in the relative importance of maintenance and growth processes. Our results emphasized that carbohydrate supply should be considered in understanding and modeling forest carbon cycling response to forest management, especially under environmental changes.

Acknowledgments

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